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# THE AMERICAN PARADOX IN THE DISTRIBUTION OF FERN TAXA ABOVE THE RANK OF SPECIES<sup>1</sup>

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## ABSTRACT

Whereas the numbers of fern species in the eastern Paleotropics and the Neotropics are comparable, the diversity at the subgeneric and especially the generic level is much higher in the eastern Paleotropics. This unexplained phenomenon is termed the "American Paradox" in the present paper.

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In editing or preparing accounts of the various fern families for the treatment of pteridophytes in the series "The Families and Genera of Vascular Plants" (Kramer et al., in press), I gave special attention to the distribution of the genera and infrageneric taxa throughout the world, especially on the major continents. The areas where genera had their major concentrations were specially noted. A somewhat unexpected picture emerged.

The poverty of species as well as superspecific taxa in the African fern flora compared with that of Madagascar, tropical Asia-Australasia, and the Neotropics is well known; it has also been documented in many groups of flowering plants. For comments and citations of further literature, see Parris (1985) for ferns and Richards (1973) for flowering plants. Another striking phenomenon, largely unnoticed, is the relative poverty of fern taxa above the rank of species in the warmer parts of the New World. In this paper I provide documentation for this "American Paradox."

## SPECIES RICHNESS

Comparing the species richness of the New World fern flora with that of tropical Asia-Australasia (leaving out Africa as much as possible for reasons stipulated above) is not easy, as few genera or families of ferns have been critically revised recently on a worldwide scale. The figures in Table 1, unless they are derived from recent monographs, should be regarded as rough approximations, mostly based on the data assembled for the "Families and Genera" referred to above. But they are probably correct regarding order of magnitude. (For the classification underlying this and other tables

and lists of taxa in the present paper, see the Appendix.) These figures show that the New World does not emerge with a poorer fern flora as a whole.

In species richness the two areas are fairly balanced, the difference in the sum being undoubtedly fortuitous. When large genera such as *Asplenium* and *Dryopteris* are revised, the balance will probably be in favor of the eastern hemisphere.

## GENERIC DIVERSITY

The picture is very different when instead of the number of species, the number of genera present in the western vs. the eastern hemisphere (excluding purely African taxa) is compared. (See Table 2.)

Note that in Lomariopsidaceae, Cyatheaceae, and Polypodiaceae, for example, where the eastern Old World and the New World have equal or at least comparable numbers of species, the number of (sub)genera is much higher in the eastern Old World. When families with fewer than four genera, where the figures are less meaningful, are left out of consideration, the difference is particularly striking: out of 13 families, 10 are considerably more diversified at superspecific levels in the Old World than in the New World; two families, Pteridaceae and Vittariaceae, are about equal; only one, Hymenophyllaceae, is more diversified in the New World. In Hymenophyllaceae the supraspecific classification is not yet completely worked out because Iwatsuki's (1984) system is based chiefly on the Asiatic representatives, so the picture may change to become even more favorable for the New World.

A comparison of Tables 1 and 2 leads to the

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conclusion that the fewer genera present in the New World contain relatively more species than the more numerous genera of the Old World. This suggests an imbalance between specific vs. generic representation.

This picture is again found when pantropical genera with very uneven distributions are compared. In Table 3 such genera are listed; they have five or fewer species in one hemisphere, the remainder in the other hemisphere.

In addition, two genera should be mentioned that, although being well represented in the Old World, have many more species in the New World, viz. *Elaphoglossum* and *Polypodium*.

INFRAGENERIC DIVERSITY

Infrageneric diversity is more difficult to assess because many subgenera and sections of ferns are treated as full genera by authors more inclined toward narrow generic circumscriptions. Here I refer to subdivisions of genera that are rarely, if ever, treated as distinct genera by contemporary authors. It proved difficult to develop reliable figures for a basis; few cosmopolitan or pantropical genera have recently been revised complete with natural infrageneric classifications. Conclusions from the following figures must be regarded as preliminary, as the number of cases is small.

*Anemia* (Schizaeaceae): see Mickel (1962, 1981) and Tryon & Tryon (1982). Three subgenera, one pantropical, one American with a single African species, one purely American. The genus was, however, more widespread in the Old World in the Tertiary (see, e.g., Huang, 1981, p. 24).

*Bolbitis* (Lomariopsidaceae): see Hennipman (1977). Ten series were proposed; three in both the Old and the New World, three only in Africa and its islands, three exclusively in the Old World (excluding strictly African taxa), one only in the New World.

*Elaphoglossum* (Lomariopsidaceae): see Mickel & Atehortúa (1980). Nine sections were recognized; four are strictly neotropical, not surprising in view of the enormous species diversity in the New World, but the five others are also represented in the Old World.

*Dryopteris* (Dryopteridaceae): see Fraser-Jenkins (1986). This comprises 16 infrageneric units (sections, or subgenera not further divided into sections); one is north-temperate, six are on both sides of the Atlantic, eight only in the eastern and one (almost) confined to the western hemisphere.

*Lindsaea* (Dennstaedtiaceae): see Kramer (1957, 1967, 1972), Kramer & Tindale (1976).

TABLE 1. Approximate numbers of species in some widely distributed fern families and genera.

Family/genus	Tropical	
	Asia-Australasia	Neotropics
Cyatheaceae	ca. 200	ca. 205
Polypodiaceae	ca. 350	ca. 250
Thelypteridaceae	ca. 440	ca. 240
<i>Adiantum</i> (Pteridaceae)	ca. 40	ca. 100
<i>Bolbitis</i> (Lomariopsidaceae)	12	14
<i>Cyclopeltis</i> (Dryopteridaceae)	ca. 5	1
<i>Elaphoglossum</i> (Lomariopsidaceae)	ca. 50	ca. 350
<i>Lindsaea</i> (Dennstaedtiaceae)	62	48
<i>Lomariopsis</i> (Lomariopsidaceae)	5	ca. 15
<i>Lygodium</i> (Schizaeaceae)	14	ca. 8
<i>Nephrolepis</i> (Nephrolepidaceae)	ca. 12	ca. 10
<i>Odontosoria</i> (including <i>Sphenomeris</i> ) (Dennstaedtiaceae)	7	8
<i>Oleandra</i> (Oleandraceae)	ca. 25	ca. 8
<i>Schizaea</i> (Schizaeaceae)	7	8
Totals	ca. 1,229	ca. 1,265

Twenty sections were recognized; two are only in the southwestern Pacific, two in Madagascar; of the others, four are present in the Old and the New World, ten in Asia-Australasia only (or, in very few cases, extending to Africa); only two are confined to the Neotropics.

*Hymenophyllum* (Hymenophyllaceae): see Iwatsuki (1984). Fifteen sections or subgenera with single sections; four are subcosmopolitan or pantropical, two only in the southwestern Pacific; of the others, four are confined to the Old World, three to the New World; here the distribution is approximately balanced.

*Osmunda* (Osmundaceae): various sources for classification. There are three subgenera, one worldwide, one north-temperate, and one in eastern Asia.

Unfortunately, no sufficiently reliable data are available for the following large, pantropical to subcosmopolitan genera where information on the distribution of their subdivisions would be useful: *Adiantum*, *Asplenium*, *Blechnum*, *Cheilanthes*, *Ctenitis*, *Diplazium*, *Grammitis*, *Polypodium*, *Pteris*, and *Tectaria*. Paleogean preponderance for supraspecific diversity seems



TABLE 2. Distribution of the genera of the fern families (excluding probable relict families). Genera not present in the tropics of Asia-Australasia and the Neotropics appear in the overall sums of genera but not in the three columns at the right.

Family	Number of genera	In both hemispheres	Old World only	New World only
Blechnaceae	9	2	4	1
Cyatheaceae (genera or sections; see Appendix)	4	3	1	0
Dennstaedtiaceae	16	11	4	1
Dryopteridaceae sens. lat.	45	18	18	9
Gleicheniaceae	5	3	2	0
Grammitidaceae	4	1	3	0
Hymenophyllaceae	8	5	1	2
Hymenophyllopsidaceae	1	0	0	1
Lomariopsidaceae	6	4	2	0
Marattiaceae	6	1	4	1
Nephrolepidaceae	1	1	0	0
Oleandraceae	3	1	2	0
Ophioglossaceae	3	2	1	0
Polypodiaceae (see Appendix)	32	5	21	6
Pteridaceae sens. lat.	33	10	11	12
Thelypteridaceae (see Appendix)	29	9	17	3
Vittariaceae	6	2	2	2
Totals	211	78	93	38

likely for *Pteris* and *Tectaria*, neogean for *Adiantum* and *Polypodium*.

At infrageneric levels, the preponderance of Asia-Australasia also seems to be present, but more weakly. This was to be expected in view of what was found for the distribution of species over the two hemispheres.

DISCUSSION

Is the “American Paradox” perhaps an artifact of different approaches of systematists working with Old World as opposed to New World ferns? It is true that certain taxonomists concentrating on Asiatic ferns have a much narrower concept of taxa on all taxonomic levels than most others; a prominent example is Ching (e.g., 1978). But the classification worked out for the “Families and Genera” from which the above figures have largely been taken is the result of a critical reevaluation of all genera. Even if this classification is not acceptable to others, it may be said with some confidence that it does not contain a bias toward either “splitting” or “lumping” for the classification of the Old World or New World ferns.

Is there an explanation for the “American Paradox”? At the moment I prefer not to make an attempt. Assuredly, the New World tropics must have been habitable for ferns as long as the Pa-leotropics, and they harbor relict taxa like Loxo-

mataceae, Gleicheniaceae, and Marattiaceae that go far back in geological history. Yet the assortment of ferns belonging to the so-called higher leptosporangiates gives the impression of relatively recent speciation in comparatively few taxa of higher rank; many of them are also present in the Old World and perhaps have originated from there. An explanation will eventually have to come from ge-ology, paleogeography, and paleoclimatology data. In light of what we know about the breaking up

TABLE 3. Genera of wide distribution but very un-evenly distributed over the world, with most species in one hemisphere, fewer than six in the other hemisphere.

Predominantly eastern hemisphere (9 taxa):	
<i>Deparia</i>	<i>Platyserium</i>
<i>Dicranopteris</i>	<i>Thelypteris</i> sect. <i>Cyclosoriopsis</i>
<i>Diplopterygium</i>	( <i>Christella</i> as genus)
<i>Lomagramma</i>	<i>Thelypteris</i> sect. <i>Stegnogramma</i>
<i>Microlepia</i>	(or <i>Stegnogramma</i> as genus)
(native in New World?)	
Predominantly western hemisphere (4 taxa):	
<i>Hemionitis</i> (the sole Old World species perhaps misplaced in the genus)	
<i>Microgramma</i>	
<i>Pleopeltis</i>	
<i>Trichomanes</i> (sensu Iwatsuki, 1984)	



of Gondwanaland, the paradox is even more perplexing. For the moment it may suffice to bring the phenomenon, duly documented, to the attention of the botanical community, without indulging in insufficiently founded speculation.

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#### APPENDIX. Notes on the classification.

As the treatment of pteridophytes for the "Families and Genera of Vascular Plants" referred to above has not appeared as this paper goes to press, certain points in the system that underlie the figures given above are briefly indicated.

Cyatheaceae: the sections upheld by Holttum in Holttum & Edwards (1983) have been counted as genera, as a compromise between the concepts of Holttum's and of R. M. Tryon's school of tree-fern students.

Dryopteridaceae: the family is broadly circumscribed, following Sledge (1973); it includes the athyrioid and the onocleoid ferns as well as *Woodsia*.

Oleandraceae: excluded from Davalliaceae (like *Nephrolepis*).

Polypodiaceae: certain species groups often treated as genera, but provisionally retained as subordinate groups of *Polypodium* in the "Families and Genera," are here counted as equivalent to genera.

Pteridaceae: these are broadly circumscribed and include *Adiantum* and all so-called gymnogrammoid ferns.

Thelypteridaceae: only five genera are retained in the "Families and Genera," but many subgenera are recognized; these are here counted as full genera in accordance with other authors' views.